A trade-off between embolism resistance and bark thickness in conifers: are drought and fire adaptations antagonistic?

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Abstract

***Background*:** Understanding the mechanisms that explain the spatial distribution of conifers across biogeographical gradients is important for anticipating potential range shifts owing to global change. Classical explanations have involved trade-offs between shade and drought tolerances, but more recent studies observed that trade-offs between fire and drought tolerances could also be important.

***Aims*:** Here we propose that a contributing mechanism to explain how conifer species are distributed across productivity gradients – with marked variation in the incidence of fire - involves a trade-off between allocation to bark, which serves to protect against fire, or to embolism resistance, which serves to protect against drought.

***Methods*:** We compiled information from different datasets and performed regression analyses.

***Results*:** We observed a trade-off between bark thickness and embolism resistance in conifer species such that species show either large investments of carbon to the bark or have thinner barks but xylem resistant to embolism; we did not observe conifer species concomitantly showing high fire tolerance and embolism resistance.

***Conclusions*:** This study serves as a starting point for a novel framework on how fire and drought adaptations affect conifer biogeography. Additional studies will be necessary to discover the generality of our findings by including other species of conifers, e.g. those in the Southern Hemisphere.

Keywords: bark, cavitation, climate change, conifers, fire, drought, life strategies, trade-off

Introduction

Variation in fire regimes (pyrogeography) across biomes is primarily driven by productivity and aridity gradients (Boer et al. 2016). Maximum global fire activity occurs at intermediate levels of productivity and aridity. Conversely, minimum fire activity is observed at sites with low productivity and high aridity (i.e. deserts, with strong fuel limitation), or at sites with high productivity and low aridity (i.e. wet

47 temperate/tropical forests, where the large amounts of accumulated biomass are seldom
48 dry enough to burn) (Keeley et al. 2012; Pausas and Bradstock 2007; Pausas and
49 Ribeiro 2013).

50 Considering these interactions between productivity and aridity as drivers of
51 pyrogeography, Keeley (2012) has proposed a division of life strategies across the
52 species of *Pinus*, later expanded by Pausas (2015), and classified species in relation to
53 fire as tolerant, embracer and avoider. Fire-tolerant species occur at the more productive
54 sites, where fire activity is often limited by high moisture that results in low intensity
55 surface fires (Figure 1). Consequently, fire-tolerant species (e.g. *P. nigra*, *P. ponderosa*,
56 *P. sylvestris*) have thick barks that allow the survival of individuals under low intensity
57 fires, but do not regenerate under high intensity crown defoliating fires. Fire-embracer
58 species occur at sites with intermediate productivity, where fire activity is highest, and
59 have a low degree of self-pruning and an overall canopy architecture that enhances
60 crown fires (Figure 1). Their regeneration depends on stand-replacing fires that open
61 their serotinous cones (e.g.: *P. attenuata*, *P. halepensis*). Fire-avoider species occur at
62 dry (or upper montane) environments, where fires are very rare and limited by fuel load
63 (or moisture), and lack adaptations to fire (e.g.: *P. aristata*, *P. uncinata*; Figure 1).

64 The analyses of trade-offs among traits have been useful to explain species
65 distributions across productivity gradients (Rueda et al. 2016; Valladares et al. 2016).
66 Here we elaborate on a mechanism that could explain, at least partly, recently reported
67 trade-offs in the ability to cope with stress (drought) and disturbance (fire) in conifer
68 species (Karavani et al. 2018; Rueda et al. 2016). We hypothesised that adaptations to
69 fire and drought incurred a cost and that conifers might not concomitantly survived
70 disturbance and stress. Thus, conifer species may either show large investments of
71 carbon to the bark, which protects the cambium and phloem against fire; or have thinner

barks and xylem highly resistant to embolism. Consequently, we hypothesised that conifer species concomitantly showing high bark thickness and embolism resistance may not occur. There are many traits involved in fire tolerance and drought resistance, but bark thickness and embolism resistance are of pivotal importance.

We begin by providing some basic calculations on the carbon costs of constructing bark and xylem resistant to embolism. We then revisit recent work indicating the potential for a trade-off between fire resistance and drought tolerance (Karavani, et al. 2018). Further, we test for the existence of a trade-off in embolism resistance and bark thickness. Finally, we explain the relevance of our findings in a broader context of conifer biogeography.

The carbon cost of constructing bark and xylem

The presence of a trade-off in the allocation of C to either building fire-resistant bark or drought-resistant xylem is conditional on the existence of substantial construction costs. Fernandes et al. (2008) have reported normalised bark thickness (the ratio of bark thickness to stem radius) in western European pines ranging from 7.4% in *P. uncinata* to 24.5% in *P. pinaster*; bark density is ca. 90% that of the xylem in pines (Miles and Smith 2009). Assuming that C concentration is similar across tissues (ca. 50% in both cases (Chave et al. 2009; Hansson et al. 2004)), it thus follows that resources consumed by the bark range from ca. 6.7 % (7.4 × 0.9) to 22.1 % (24.5 × 0.9) those of the xylem, thus representing a substantial construction cost.

In terms of embolism resistance, different adjustments of tracheid anatomy and morphology occur for different conifer families. In species of the Pinaceae and Cupressaceae (which largely dominate our analyses), wood density and tracheid 'thickness-to-span' ratio are strongly correlated with protection from drought-induced embolism (Pittermann et al. 2006). Consequently, mechanical strength is required in

97 these species to avoid tracheid collapse under drought and the correlation between
98 density and resistance to embolism indicates that these trees incur substantial C costs
99 during xylem construction [i.e.: higher wood density leads to higher embolism
100 resistance; (Pittermann, et al. 2006)]. In fact, recent studies have demonstrated that the
101 amount of lignin, which varies between 25 and 36% of wood dry mass in conifers
102 (Fengel and Grosser 1975; Pettersen 1984), is directly related to embolism resistance.
103 Pereira et al. (2017) have observed a significant correlation between the values of Ψ_{50}
104 (the xylem potential where 50% of the hydraulic conductivity is lost) for different
105 species (Choat et al. 2012) with their respective lignin concentrations (Fengel and
106 Grosser 1975; Pettersen 1984). Based on such correlation, they quantified that an
107 increase of 1% of dry mass allocation to lignin reduced Ψ_{50} by -0.3MPa.

108 **Evidence for trade-offs in embolism resistance and fire tolerance in conifers**

109 The existence of a trade-off between fire tolerance and cavitation resistance in conifer
110 species may be tested with previously published datasets. Data on embolism resistance
111 were obtained from a global database (Choat, et al. 2012). We used Ψ_{50} as this is a
112 commonly used indicator of embolism resistance in conifers (Brodribb and Cochard
113 2009). We collected data on fire tolerance from the USDA PLANTS database
114 (www.plants.usda.gov, 13 Dec 2016). This database provides a value on "the relative
115 ability to resprout, regrow, or re-establish from residual seed after a fire", and there are
116 four possible levels (none, low, medium, high). After crossing the two datasets, we were
117 able to examine hydraulic resistance and fire tolerance across 41 conifer species (Table
118 S1). No species from those present in the database was able to resprout.

119 In this analysis we found evidence for a trade-off between Ψ_{50} and fire tolerance
120 (Figure 2a). Conifers with xylem more resistant to embolism (e.g. with $\Psi_{50} \leq$ -6 MPa,

and down to -12MPa) had either low or no tolerance to fire (levels 1-2 in Figure 1a), whereas conifers with mid or high fire tolerance (levels 3-4 in Figure 2a) always showed smaller embolism resistance (e.g. with Ψ_{50} > -5 MPa) (Figure 2a). We also observed some conifer species with low resistance to cavitation and low tolerance to fire but there were no species showing both high fire tolerance and high Ψ_{50} (Figure 2a). Despite the scatter in the data, the lack of conifers concomitantly showing high fire tolerance and high embolism resistance points towards a trade-off between these two traits.

As proposed by Grubb (2016), the existence of trade-offs may be formally demonstrated through quantile regression (when fitting an upper quantile the regression becomes significant). Consequently, we examined the significance of the 0.5, 0.75 and 0.95 quantiles and found only the 0.95 quantile regression significant ($P < 0.05$) (using the "quantreg" package (Koenker 2016) within the R software environment (R Core Team 2016)), hence suggesting a trade-off between Ψ_{50} and fire tolerance in conifers (Figure 2a). We note that using different datasets could introduce additional uncertainty around mean trait values. However, this problem affected equally all species and should not lead to any systematic bias.

Evidence for trade-offs in embolism resistance and bark thickness in conifers

The previous analysis is not exempt of criticism because of the ambiguous definition of fire tolerance in the USDA PLANTS database. To overcome this limitation, we conducted further analyses with independent sources of information to test the specific hypothesis that there was a trade-off in the allocation of resources to the bark or to embolism resistance. First, we digitised data on resistances to cambium kill from a previous study on fire resistance across European pines (Fernandes, et al. 2008). This

allowed the examination of six species in total (Table S1), a small number, but respresenting a substantial proportion of the pines in Europe (Barbéro et al. 1998; Willis et al. 1998). Cambium kill resistance in the study by Fernandes, et al. (2008) was derived from the percentage of tree radius occupied by bark (at 1.3 m). We observed a negative relationship between resistance to cambium kill and Ψ_{50} (Figure 2b), which is consistent with our hypothesis of a trade-off.

We additionally used an independent dataset on bark thickness at a normalised stem diameter of 10 cm across 20 conifer species (Table S1) from a recent global study (Pellegrini et al. 2017). We observed again that species with a thicker bark were least resistant to embolism and there were no species concomitantly showing thick bark and high embolism resistance (Figure 2c). While more data would be needed to generalise this claim, the trade-off is formally anticipated by the significant (at $P < 0.05$) 0.95 quantile regression.

We also addressed patterns of intra-specific genetic variation underlying a potential trade-off between drought and fire tolerances by digitising graphs with data on bark thickness (Tapias et al. 2004) and on Ψ_{50} (Corcuera et al. 2011) for six different provenances of *P. pinaster* grown under uniform conditions. This Mediterranean pine has a very broad ecological niche (from sea level to 1900 m), which has elicited adaptive divergence among populations arising through localised selection (González-Martínez et al. 2004). The provenances spanned a broad precipitation (348 - 1,257 mm yr^{-1}) and soil fertility gradient (mainly acid soils, but also basic soils and even sandy and poor soils such as those of Landes, France). From a fire perspective this species is important as a large proportion of all fires in the western Mediterranean basin occur in *P. pinaster* stands. In Spain alone, one-third of all forest fires have been reported from forests dominated by this species (MAGRAMA 2012). This dataset, at intra-specific

level, once more indicated a negative relationship between bark thickness and Ψ_{50} was also significant (Figure 2d).

Conclusions and outlook

Overall, our analyses using independent datasets and across different geographical scales indicate that there are no conifers concomitantly showing high embolism resistance and high tolerance to fire and that this may be owing to an C allocation trade-off between bark and lignin. Moreover, the intra-specific association observed for *Pinus pinaster* under common-garden conditions (Figure 2d) indicates that this trade-off has a genetic basis, although further studies on genetic variation would be required to generalise this claim.

Our hypothesis on a trade-off between embolism resistance and fire tolerance raises the question as to whether adaptations to fire and to drought may, at least to some degree, be antagonistic in conifers. This hypothesis is still tentative because many additional mechanisms, including stomatal regulation, root:shoot allocation or stem capacitance to name a few, are also involved in drought resistance. However, it could provide a mechanistic explanation, at least partially, to the distribution of the species of *Pinus* and, in general, conifers with different life strategies across productivity gradients (Rueda, et al. 2016).

Further studies should address the role of site fertility as an additional driver of productivity. From the perspective of pyrogeography, productivity gradients have so far been defined as precipitation gradients (Pausas and Bradstock 2007). However, site productivity is also a function of nutrient concentrations and that could be particularly important for species that occurg across a wide range of soil nutrient availabilities (e.g.: *P. pinaster*, *P. sylvestris, Larix laricina, Taxodium distichum*, etc). This is particularly

194 important because nutrient concentrations tend to decrease xylem vulnerability to
195 embolism (Ewers et al. 2000; Resco de Dios et al. 2013), although less is known on its
196 effects on bark production or fire tolerance, and also because of human-induced nutrient
197 imbalances such as nitrogen deposition (Ochoa-Hueso et al. 2011).

198 Fire-embracing species, that occupy intermediate productivity sites, would need
199 a high resistance to drought because they are regularly exposed to periods of water
200 scarcity, but they also live in crown-fire environments and, since non-resprouting trees
201 often succumb under high intensity crown defoliating fires, any carbon investment into
202 building structures enhancing fire survival may be futile. Consequently, the mechanism
203 that allows the maintenance of these species in such environments, rather than cambium
204 or crown adaptations to withstand fires, relies on a reproductive strategy that ensures
205 post-fire seed availability via an aerial seed bank (i.e. serotinous cones) (Martín-Sanz et
206 al. 2016). Similarly, fire-avoiding species from arid environments (e.g. *P. edulis, P.*
207 *monophylla*), which likely show the highest drought tolerance, often lack fire
208 adaptations (Keeley 2012). Additionally, fire-avoiding upper montane treeline-forming
209 species which experience cavitation caused by freeze-thaw cycles notably also lack fire
210 adaptations. Conversely, mesic conifer species need protection from surface fires but
211 are less exposed to periods of intense drought and, consequently, may preferentially
212 allocate more resources into protecting the phloem and cambium than the xylem.
213 Considering forecasts of increased drought and fire occurrence across parts of the
214 geographical range of temperate conifers (Moritz et al. 2012), understanding conifer
215 strategies for dealing with these factors should be at the forefront of our research efforts.
216 Subsequent work should also address the possibility of recovery from cavitation either
217 by stem refilling or by resprouting.

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Notes on contributors

Víctor Resco de Dios is interested in understanding biological processes regulating biosphere-atmosphere interactions.

Carles Arteaga is interested in post-fire regeneration processes.

Javier Hedo is interested in understanding the effects of fire on forest soils.

Eustaquio Gil-Pelegrín is interested in whole-plant ecophysiology of woody plants, especially in the functional responses of trees and shrubs to drought.

Jordi Voltas is interested in understanding adaptive patterns of Mediterranean conifers and their implications for species resilience under global change

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Figure legends

Figure 1: Idealised and simplified representation of how different conifer functional groups are distributed across productivity gradients according to a presumed trade-off between fire tolerance and embolism resistance.

Figure 2: Trade-offs between embolism resistance and bark thickness. (a) Relationship between fire tolerance (1, none; 2, low; 3, medium; 4, high; from PLANTS USGS database) and the xylem potential where 50% (Ψ_{50}) of the hydraulic conductivy is lost (Choat, et al. 2012) across 41 conifer species. (b) Relationships between cambium and kill resistance (in relative units) (Fernandes, et al. 2008), against the xylem water potential where 50% of the hydraulic conductivity is lost (Ψ_{50}) (Choat, et al. 2012) across six European pine species. (c) Relationship between bark thickness for a diameter of 10 cm (Pellegrini, et al. 2017) against the xylem potential where 50% of the hydraulic conductivity is lost (Ψ_{50}) (Choat, et al. 2012) across conifer species. (d) Relationship between bark thickness (Tapias, et al. 2004) and Ψ_{50} (Corcuera, et al. 2011) across six *Pinus pinaster* provenances. The line indicates results of quantile (a, c) or linear (c, d) regression. *P*-values and R^2 are given for quantile and linear regression, respectively. In quantile regressions, we examined the significance of the 0.5, 0.75 and 0.95 quantile regressions for all plots but only the 0.95 quantile regressions were significant at $P < 0.05$, as indicated by the plotted line. X-axis scales may differ between panels. (a) modified from (Karavani, et al. 2018).